THE SUBDIVISION OF ASCLEPIADACEAE

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Introduction

In 1809 Robert Brown separated a group of genera from
the Apocyneae (= Apocynaceae) on the basis that they
differed from the remainder of the family in possessing
free styles, a gynostegium (i.e. the fusion product of
the androecium and gynoecium or parts of them), pollen
masses and the more or less common presence of an extra
whorl of corona attached in various forms to the petals.
He named this group the Asclepiadeae. Apart from these
differences, the Apocyneae sensu stricto and the then
newly emerging Asclepiadeae shared a multitude of attr-
ibutes, viz. the regular, pentamerous, tetracylic,and
hypogynous flowers, the almost universal presence of
latex and the contorted imbrication of petals. Eversince,
the Asclepiadeae grew in size to accomodate new genera
and species, and their name was subsequently changed by
Lindley (1853) to Asclepiadaceae R.Br.

The Asclepiadaceae were first classified by Decaisne
(1844) into 5 tribes (Periploceae, Secamoneae, Asclepi-
adeae, Gonolobeae and Stapelieae) on the basis of pollen
structure, with the first tribe having pollen in tetrads
while all other 4 tribes are characterized by pollen
masses or pollinia. The mechanism of pollen discharge
differs also in the Periploceae (where the tetrads are
received and dispersed by spathulate translators) than
in the rest of the family (where the pollinia are atta-
ched to glandular secretions known as corpuscles from
the 5 corners of the pentagonal stigma via non-cellular
cords known as the caudicles or connectors). Decaisne's
classification was later accepted in its entirity by
subsequent taxonomists (e.g. Lindley 1853). However,
the subdivision of Asclepiadaceae sensu Decaisne has
undergone a number of alterations involving primarily
the hierarchical status of each of the 5 tribes. While
some authors (e.g. Schumann 1895, Rendle 1925, Melchior
1964) prefer to split them into only two subfamilies
the Periplocoideae (= Decaisne's tribe Periploceae) and

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Cynanchoideae (= the other 4 tribes), within the Asclepiadaceae s.l., Schlechter (1924) and most subsequent authors (e.Bullock 1957, Huber 1967, Dyer 1975) promote the former subfamily to family Periplocaceae, with only the Cananchoideae forming the Asclepiadaceae s.s. Genera of the latter group are then arranged into 2 subfamilies the Secamonoideae (with a pair of pollinia in each anther lobe) and the Cynanchoideae s.s. or Asclepiadoideae with only one pollinium in each anther lobe. Both opinions continue to gain advocates so that no general agreement among taxonomists regarding the circumscription of the Asclepiadaceae seems to prevail.

The Asclepiadaceae s.l. are a relatively large family with 250-320 genera and 1700-3000 species (see Rendle 1925, Willis 1931, Melchior 1964, Schill & Jäckel 1978), of which only about 45-50 genera and 200 species constitute the Periplocaceae while the rest fall in the Asclepiadaceae sensu stricto. A highly conservative estimate of the number of genera in the family is given by Airy Shaw (1973) as 130, but it has not been shared by any other taxonomic account of the family. The discrepancy concerning the number of genera and species reflects an unstable taxonomic situation within the family and it can easily be felt that both generic and specific concepts in the Asclepiadaceae are far from satisfactory. It is also noticeable that the distribution of the species among the genera is highly uneven. Thus all the genera listed by Airy Shaw (1973) have been surveyed together with their reported numbers of species and it has been found that there are no less than 123 mono-specific genera (i.e. 38.4 %), 118 genera (i.e. 37 %) each with 2-10 species, and only 16 genera (5 %) take in about 1800 species (i.e. approx. 60 % of all the species in the family).

In view of their unambiguous taxonomic boundaries, the Asclepiadaceae would have been expected to be among the more attractive targets for comprehensive taxonomic studies. On the contrary, the existance of only one main classificatory treatment of the family (with only superficial differences about hierarchical rank of the subordinate groupings) and its perpetuation in all text-books and floristic works shows that the asclepiads are long due for a thorough taxonomic reappraisal, especially in view of the fact that numerous genera and species have been described after the publication of Schumann's (1895) scheme. Furthermore, owing to the probably erroneous belief that the Asclepiadaceae are of little or no economic importance, this family has been grossly neglected from various botanical standpoints for a long

time. This is clearly manifest in the fact that although
this group is unique among angiosperms in their pollen
structure and pollination mechanism, and that it was
originally created and subdivided into smaller taxa
because of their pollen peculiarities, they remained
without a comprehensive study of their pollen morphology
until attention has recently been drawn by El-Gazzar &
Hamza (1973), and El-Gazzar, Hamza & Badawi (1974) to
this obvious neglect of the family by palynologists. It
is only when it became clear that the family has plenty
to offer from the palynological standpoint that some
interest has been in them by Schill & Jäckel (1978),
whose efforts materialized in an excellent comparative
account of various pollen morphological features of a
relatively large sample of 408 species from 114 genera
representing the Asclepiadaceae sensu lato. Nevertheless
the wealth of information reported by Schill & Jäckel
has not as yet been put to any practical use in establ-
ishing the taxonomic worth of existing classifications
of the family. Other sources of phenotypic variation
remain virtually untapped.

With the foregoing remarks in mind we have set out to
investigate as many aspects of variation as can be obse-
rved in a large representative sample of genera and
species, and to benefit from the recorded observations
in (a) assessing the value of existing classifications,
and (b) achieving a more meaningful arrangement of the
genera which would cater for those described after the
publication of Schumann's (1895) system. It should be
pointed out that the scope of the present work has been
limited only to the Cynanchoideae (by far the larger of
the two subfamilies of Asclepiadaceae sensu stricto),
and that a separate detailed study of the Secamonoideae
is currently in progress.

General account of Cynanchoideae

The plants are generally small erect perennial herbs,
herbaceous or woody twiners or scramblers, with a number
of leafy or leafless succulent or cactus-like genera
(e.g. Caralluma, Hoodia, Huernia, Huerniopsis, Stapelia,
Stapeliopsis). The presence of latex is universal in
the subfamily, and some species (especially from Stape-
lia) have an exceedingly foetid smell similar to that of
rotten meat. The leaves are almost invariably simple
and exstipulate, but may be opposite, whorled or rarely
alternate. The flowers are usually arranged in dense
dichasial cymes, racemes or umbels; partial inflorescences
are mostly axillary and in acropetal succession along
the stem although sometimes the plant carries only one

simple (often sessile) terminal umbel (as in some succu-
lents, e.g. Caralluma, Boucerosia), or the flowers may
be few, ebracteate and born singly on the cactus-like
stem of some Stapelia, Hoodia, Huernia, Trichocaulon and
Duvalia species.

The flower is constantly regular, pentamerous, tetra-
cyclic, hermaphrodite and hypogynous. The calyx consists
of 5 free imbricate sepals, which may be minute and ind-
istinct (e.g. some Cynanchum spp.). The petals are 5,
constantly united though to greatly variable degrees;
the limbs range from much reduced to considerably longer
than the tube. Petal limbs are contorted in bud, but
after anthesis assume numerous shapes ranging between
horizontally stellate (e.g. Stapelia), elongate to more
or less filiform (e.g. Ceropegia, Araujia, Riocreuxia),
and recurved triangular (e.g. Asclepias). The androecium
consists of 5 stamens furnished with a staminal corona
which takes almost as many shapes as there are species
in the subfamily; hence its utmost identificatory value.
The gynoecium is made up of 2 median superior carpels
whose ovaries and styles are free, while the stigmas are
united into a relatively large pentagonal body with or
without a simple or conspicuously bifurcate apical appe-
ndage. Each locule contains a few to several multiser-
iate anatropous and pendulous ovules. The fruit consists
of 2 separate follicles, each with a few-several flatt-
ened exalbuminous seeds with smooth or glossy pale yellow
to brown testa and a distal tuft of silky white hairs.
The outer surface of each follicle may be smooth, finely
felty or provided with a number of hook-shaped soft
outgrowths. The 5 staminal filaments are adnate to each
other and to the style apex. Each anther consists of 2
unilocular anther-lobes and lies opposite to one side of
the pentagonal stigma. At each of the 5 corners of the
stigma a horny non-cellular secretion is produced and is
known as the corpuscle (or corpusculum). It is attached
to a pair of pollinia (via two non-cellular caudicles),
each from one lobe of the 2 adjacent anthers. Therefore,
although each of the 2 pollinia attached to the same
corpuscle belongs to a different anther, they are both
morphologically identical and are released from their
respective thecae simultaneously and have been termed
"twin pollinia" by El-Gazzar & Hamza (1973); a term later
adopted by Schill & Jäckel (1978). Each corpuscle with
2 caudicles and a pair of twin pollinia is generally
known as the pollinial apparatus.

The development of pollinial apparatus in the Ascle-
piadaceae is a floral modification to facilitate as well
as ensure both cross-fertilization and entomophily. Thus

a visiting insect rests on the glandular or slippery
surface of the stigma and attempts to reach down for the
nectar, its legs fall between the anthers and in trying
to retrieve them they detach the corpuscles from the
stigma. The twin pollinia are thus released from their
thecae together with the corpuscles through the agency
of the caudicles. The same insect transfers its load of
pollinial apparatus to another flower, and keeps exchan-
ging pollinia between various flowers of the same species.
The pollen tubes from the same pollinium all enter one
of the two ovaries in the flower (Frey 1902). We have
not been able to find any detailed account of the insects
aiding in the pollination of asclepiads, and the quest-
ion whether there is any specificity between insect and
plant species or genera and the factors governing such
insect-plant relationship (if any) remaines unresolved.
However, according to Knuth (1898) the insect pollinators
of the following genera are:

    Asclepias: flies ("Fliegen"), bees ("Bienen"), wasps
               ("Wespen"), tomb-wasps ("Grab-wespen").
    Araujia: large bees ("grosser Bienen").
    Stephanotis: long-trunked moths ("lang-russeliger
               Schwärmer").
    Stapelia: carrion-flies ("Aasfliegen").
    Ceropegia: small flies ("kleine Fliegen").

Modifications in the flower to suite insect pollination
seem limitless and involve other whorls as well. The
accessory organs (such as staminal and corollary corona)
and the presence of pollinia in the upper or lower parts
of the anther-lobes are among such modifications.

    According to Good (1952) the Asclepiadaceae are found
throughout the tropics and over a considerable part of
the warmer temperate regions, with a notable exception
that they are absent from much of the Pacific including
the Hawaiian Islands. In North America they are throug-
out the United States and enter Southern Canada on a wide
front, reaching at one point a latitude of nearly 60 N.
In the northern Old World they are absent from the Azores
and from the British Isles, but occur throughout the
rest of Europe,except for a few small coastal areas, as
far north as latitude 61 N in southern Finland. In the
southern hemisphere the boundary runs obliquely across
South America to a latitude short of 50 S, includes all
Africa, and virtually all Australia, though not Tasmania
and New Zealand. Some adventive species such as Asclep-
ias curassavica, Gomphocarpus fruticosus and Calotropis
procera are found in nearly all warmer parts of the
world, including some areas where the family is not
native. The proportion of narrowly distributed or

endemic genera is very high and some are very local. The
proportion of narrowly distributed or endemic species is
even higher and there is no species common to both worl-
ds.   The areas of greatest relative species concentration
are first and formost South Africa, and to a lesser
degree the Madagascar region and Malaysia.   Although
Good offered no explanation for the peculiar phenomena
of total absence of asclepiads from most islands and the
very high incidence of narrowly distributed or endemic
genera and species, it seems that the spreading of such
plants is highly dependent on the presence of a specific
insect or group of insects for pollination which may be
highly localized or may not find it easily palatable to
inhabit most islands with their predominently severe
environmental conditions.

For over 160 years the work on pollen morphology in
the Asclepiadaceae was confined to brief descriptions and
inadequate illustrations of the pollen apparatus in a
few individual species by Frye (101), Volk (1949), and
Dassanayaka & Jayasuriya (1974).   The work of Huang
(1970) on some Formosan species deserves a special ment-
ion here as it incorporates a number of basic and clear
errors.   Thus despite the universal belief that the
Cynanchoideae are definable by the presence of pollinia
attached in pairs to stigmatic corpuscles through non-
cellular caudicles, Huang described the pollen of 3 of
the 7 species studied by him (Cynanchum formosanum,
Hoya carnosa and Stephanotis mucronata) as 3(-6) porate
or colporate monads, and of the rest as "polyads", with
no mention of pollinia, caudicles or corpuscles in any
of them.   Furthermore, the dimensions given by Huang for
the "polyads" of the remaining 4 species (Gymnema
alternifolia, Marsdenia tomentosa, Tylophora breviper,
Wattakaka volubilis) are at variance with those given
for the same species by El-Gazzar & Hamza (1973),
El-Gazzar et al (1974) and Schill & Jäckel (1978). Under
the circumstances, one cannot help feeling that Huang
might have gone astray with the identification of the
specimens available to him, or that Formosan asclepiads
are yet to be thoroughly revised.

The lack of interest in the Asclepiadaceae is further
exemplified by the small fraction of genera and species
studied cytologically.   According to Cave (1956-1964),
Fedorov (1969), Ornduff (1967, 1968) and Moore (1973-
1977), chromosome numbers have been reported for only 46
genera and slightly more than 200 species (ca. 6.6 % of
the total in the family).   This may be attributable, at
least in part, to the fact that the family is cytologic-
ally almost entirely homogeneous, with nearly all the

species studied so far having chromosomes in multiples
of 11, with a few dubious records of 2n = 24.

Similarly, little is so far known about the embryol-
ogy of the plants. The micro- and macro-sporogenesis,
including embryo sac and endosperm development, in
Asclepias were dealt with by Gager (1902), and in Calot-
ropis procera by Sabet (1931). Another detailed study
of 8 Asclepias species and 2 Acerates species was made
by Frye (1902). According to his observations, groups
of 1-6 non-nectariferous glands occur between the calyx
and corolla, and near the axils of sepals, bracts and
leaves; they may also be found on leaf midribs.   Frye
also reported double-fertilization in Asclepias cornuti,
that the seed pappus is formed of single-celled, uninuc-
leate epidermal hairs, and that the ovules in Asclepiad-
aceae are unitegmic, with the nucellus consisting of one
layer of cells enclosing the sporogenous row and may
contain nucellar tracheids.

Material and observations

We have been able to procure fresh and herbarium
specimens of 510 species from 148 genera representing
all tribes and subtribes of the Cynanchoideae in Schuma-
nn's classification (1895). Herbarium material has been
obtained from the herbaria of Cairo University, Liverpool
University, the Botanical Museum (Copenhagen), and the
Institutes of Systematic Botany at Lund and Munich. The
correct identification has been ensured by various means:
(i) the examination of as many specimens carrying the
same name as possible, (ii) local and regional floras,
and (iii) matching with type or iso-type material.

The specimens have been subjected to a detailed
comparative investigation and 59 aspects of discontinuous
variation have been recorded for every species. The
result is a voluminous data-matrix, of which copies are
available on request. It will suffice here only to list
the recorded characters (Table 1). They cover features
from gross vegetative morphology, floral structure,
epidermal patterns, types and distribution of calcium
oxalate crystals (prismatics and druses) as well as the
variation in structure and configuration of the different
parts of the pollinial apparatus. Although most of the
characters are self-explanatory, some are novel or less
familiar and are in need of some clarification; for
detailed description and illustration of all pollinial
features reference may be made to El-Gazzar & Hamza
(1973), El-Gazzar et al (1974), and Schill & Jäckel
(1978).

Table 1. List of the 59 characters recorded comparatively
for 510 species from 148 genera of the Asclepiadaceae-
Cynanchoideae.

Stem:	1.	erect / twining or scrambling
	2.	succulent / not so
Leaves:	3.	present / absent
	4.	petiolate/ sessile-subsessile
	5.	opposite / otherwise
	6.	ovate-elliptical / lanceolate-linear
	7.	margin entire / not so
	8.	margin flat / recurved
	9.	associated stomata, present / absent
hairs:	10.	unicellular, present / absent
	11.	multicellular uniseriate, present / absent
	12.	multicellular multiseriate, present / absent
	13.	glandular, present / absent
crystals:	14.	druses, present / absent
	15.	prismatics, present / absent
Inflorescence:	16.	umbel / otherwise
Flowers:	17.	corolla stellate / campanulate
	18.	petal limbs recurved / flat or erect
Pollinia:	19.	tail, present / absent
	20.	longitudinally symmetrical/asymmetrical
Caudicle:	21.	corona present / absent
	22.	wing present / absent
	23.	horned / not so
	24.	attachment to corpuscle basal/lateral
	25.	2 lateral arms present / absent
Calyx:	26.	druses present / absent
	27.	prismatics present / absent
	28.	unicellular hairs present / absent
	29.	uniseriate hairs present / absent
	30.	glandular hairs present / absent
	31.	multiseriate hairs present / absent
Corolla:	32.	druses presnt / absent
	33.	prismatics present / absent
	34.	unicellular hairs present / absent
	35.	uniseriate hairs present / absent
	36.	glandular hairs present / absent
	37.	petals caudate / otherwise
	38.	druses in corona present / absent
	39.	corona hairy / glabrous
Gynoecium:	40.	druses in ovary-wall present / absent
	41.	ovary hairy / glabrous
	42.	druses in style present / absent
	43.	style hairy / glabrous
	44.	druses in stigma present / absent

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                45. stigma hairy / glabrous
                46. stigma appendaged / not so
Indumentum:     47. glabrous/hirsute/tomentose/spiny
Leaf-apex:      48. acute/acuminate/obtuse/notched
Leaf-base:      49. cordate/rotundate/decurrent
Stomata:        50. tera-/hexa-/anomo-/actinocytic
Corona:         51. darker than petals/petals darker/both of
                    the same colour
Pollinia:       52. length in u
                53. breadth in u
                54. P/C ratio (pollinium length/corpuscle
                    length)
                55. pendulous/erect/horizontal
                56. tail distal/basal/lateral inner/lateral
                    outer
                57. attachment to caudicle terminal/
                    subterminal/median
Corpuscle:      58. length in u
                59. breadth in u
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Epidermal trichomes in the Cynanchoideae are invaria-
bly in the form of hairs and no scales have been seen in
the species examined. These hairs show great structural
diversity so that the following basic types can easily
be recognized:

(i) unicellular: Figs. 1-3,
(ii) multicellular, uniseriate eglandular: Figs. 4-6,
(iii) multicellular, uniseriate glandular: Figs. 7-9,
(iv) multicellular, multiseriate eglandular: Fig. 10,
seen in only 5 species (Gomphocarpus appendiculatus,
Xysmalobium dilatatum, Schubertia schreiteri, Schizoglo-
ssum bidens and Rothrockia cordifolia). Furthermore, in
addition to the 4 basic types of stomata (tetracytic,
anomocytic, hexacytic in Fig. 11, and actinocytic) as
defined by van Cotthem (1970, 1971), associated (or
contiguous) stomata (Fig. 12) have also been seen in 26
species from 16 genera. As far as we are aware this is
the first recording of associated stomata in the Asclep-
iadaceae.

It should be pointed out that our observations on the
pollinial apparatus coincide to a large extent with those
of Schill & Jäckel (1978). However, there are some minor
discrepancies concerning the dimensions of pollinia and
corpuscles, which may be due to one or more of the
following reasons: (i) incorrect identification of the
plants, (ii) while we had to work mostly with herbarium
specimens Schill & Jäckel used fresh material of most of
the species in their sample and the flowers may not have
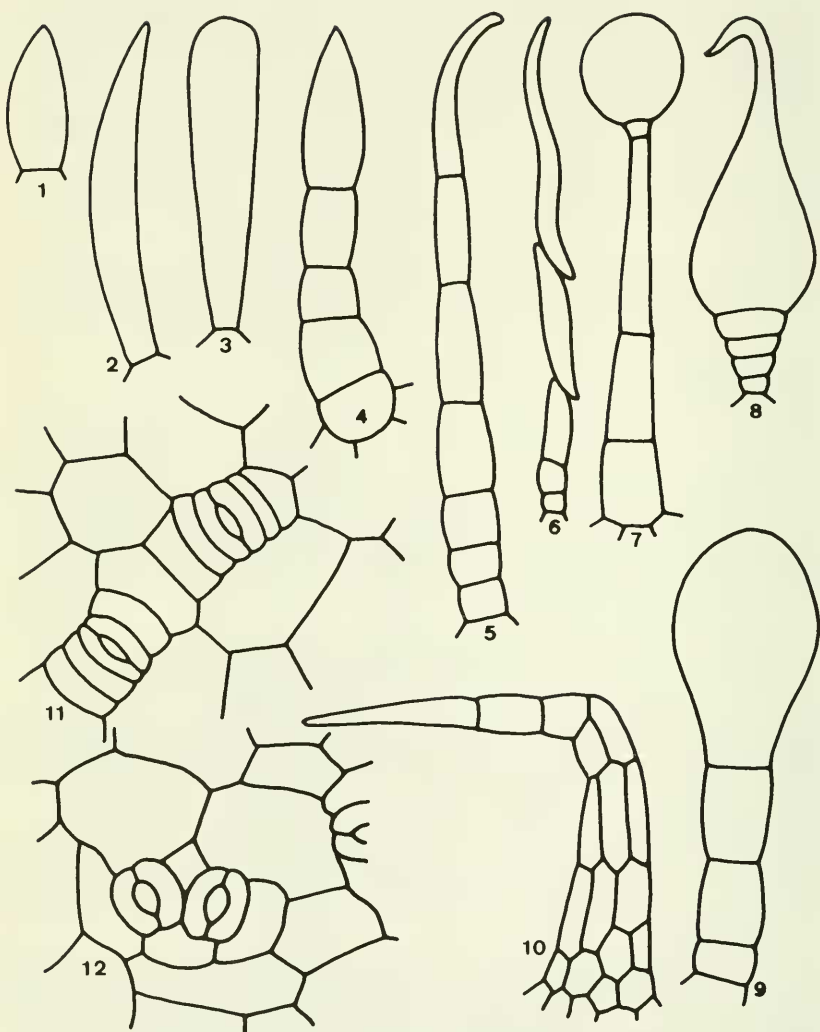
Figs 1-12. Diagrammatic representation of stomata and trichomes in Cynanchoideae. Figs. 1-3 unicellular hairs; Figs. 4-6 multicellular uniseriate hairs; Figs. 7-9 multicellular glandular hairs; Fig. 10 multicellular multiseriate hair; Fig. 11 hexacytic stomata; Fig. 12 associated stomata.

attained a fully mature stage in their development, (iii) the pollinia may not have been places on the slides in the correct position for measurement, (iv) our pollen preparations have been made without resort to the hazardous, complicated and time-consuming acetloysis technique used by Schill & Jäckel, which is bound to affect all pollinial measurments.

Taxonomic discussion

In an attempt to test the various taxonomic treatments of the Cynanchoideae in the light of the recorded observations, the data-matrix has taken different forms during the various stages of the work. Originally the species have been arranged according to the classification of Decaisne (1844) and the percentage distribution of each character in all of his groupings has been calculated. It soon became apparent that Decaisne's system is not only inadequate for accomodating the multitude of genera described after it was published, but also incapable of imposing any discernible pattern on the recorded observations. Decaisne's classification is therefore excluded from further discussion.

The species have then been re-arranged according to the currently accepted classification of Asclepiadaceae by Schumann (1895) and the same procedure of calculating the percentage distribution of the characters in each group has been repeated. Although Schumann's scheme represents a marked betterment over that propsed by all his predecessors, the present test showed clearly that there is plenty of room for improvement in it. We have therefore set out to re-arrange the data-matrix in order to achieve groupings that are as homogeneous as possible irrespective of all other classifications of the family. In doing so, we have been backed by the comfortable feeling that our data-matrix is the largest set of comparative observations yet scored for the Cynanchoideae both in terms of the number of taxa and the number of characters recorded for them.

Three major groups (A, B and C) can easily be recognized as follows (see also Table 2):

GROUP A: Herbs, commonly erect; pollinia pendulous, never with extra-pollinial appendages; terminal attachment of caudicle to pollinia; P/C ratio usually 2.5 or more; petal lobes recurved.

GROUP B: Mostly scrambling or twining herbs or shrubs; pollinia generally smaller than in A, often erect (sometimes pendulous or horizontal); extra-pollinial appendages frequent (as distal or basal tail);attachment

Table 2. Distribution of 148 genera of Asclepiadaceae-
Cynanchoideae among groups A-C as compared to the tribes
and subtribes in Schumann's (1895) classification.
Figures in parentheses represent the total number of
genera in each of groups A-C, the number of genera stud-
ied from each tribe or subtribe, or the number of species
examined from each genus. Genera not known to Schumann
are listed as unclassified.

GROUP A (39)

Asclepiadeae-Astephaninae (6): Amblystigma (1), Astepha-
nus (4), Hemipogon (1), Microloma (8), Mitostigma
(3), Nautonia (1)

Asclepiadeae-Glossonematinae (7): Araujia (4), Macrosce-
pis (1), Oxystelma (2), Parapodium (1), Prospostelma
(1), Rhyssostelma (1), Solenostemma (1)

Asclepiadeae-Asclepiadinae (19): Acerates (3), Asclepias
(82), Blepharodon (2), Calotropis (2), Cordylogyne
(1), Eustegia (1), Gomphocarpus (12), Kanahia (3),
Lugonia (1), Madarosperma (1), Margaretta (3),
Melinia (1), Pachycarpus (5), Pycnostelma (2),
Stathmostelma (1), Stenostelma (1), Tassadia (1),
Trachycalymma (1), Xysmalobium (8)

Asclepiadeae-Cynanchinae (2): Holostemma (1), Pleurost-
elma (1)

Unclassified (5): Amblyopetalum (1), Aphanostelma (2),
Dorystephania (1), Oxylobium (1), Widgrenia (1)

GROUP B (100)

Asclepiadeae-Glossonematinae (6): Ceramanthus (1),
Fischeria (2), Glossonema (2), Philibertia (1),
Schubertia (2), Steinheilia (1)

Asclepiadeae-Asclepiadinae (11): Ampelamus (1), Ditassa
(8), Enslenia (2), Funastrum (7), Macroditassa (1),
Metastelma (17), Pentarrhinum (3), Podostelma (1),
Raphistemma (1), Schistogyne (1), Schizoglossum
(22)

Asclepiadeae-Cynanchinae (19): Cyathostelma (1),
Cynanchum (35), Cynochtonum (1), Daemia (1), Deca-
nema (1), Endotropis (1), Glossostephanus (1),
Mellichampia (1), Metaplexis (2), Morrenia (3),
Orthosia (3), Pentatropis (2), Peplonia (1),
Roulinia (3), Sarcostemma (6), Sattadia (1), Seut-
era (1), Telosma (1), Vincetoxicum (5)

Asclepiadeae-Oxypetalinae (5): Calostigma (4), Gothofreda

Table 2 (cont.)

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(1), Oxypetalum (19), Rojasia (1), Tweedia (1)

Tylophoreae-Ceropegiinae (8): Anisotoma (1), Brachystel-
ma (4), Ceropegia (12), Echidnopsis (1), Leptadenia
(5), Orthanthera (1), Riocreuxia (3), Sisyranthus
(3)

Tylophoreae-Marsdeniinae (24): Barjonia (2), Cosmostigma
(1), Dischidia (2), Dregea (2), Fockea (1), Gongro-
nema (2), Gymnema (4), Heterostemma (2), Hoya (9),
Jobinia (2), Lorostelma (1), Marsdenia (11),
Nephradenia (1), Pentasacme (1), Pergularia (1),
Petalostelma (1), Rhyssolobium (1), Sarcolobus (2),
Sphaerocodon (2), Sphinctostoma (1), Stephanotis
(1), Tenaris (1), Treutlera (1), Tylophora (9)

Gonolobeae (15): Chthamalia (1), Dictyanthus (4),
Exolobus (2), Fimbriostemma (1), Gonolobus (10),
Himantostemma (1), Ibatia (2), Malinvaudia (1),
Matelea (3), Peckoltia (1), Phaeostemma (1), Phera-
trichis (2), Rothrockia (1), Trichosacme (1),
Trichostelma (1)

Unclassified (12): Clemensiella (1), Dalziella (1),
Diploplexis (1), Glossostelma (1), Gonianthela (1),
Gynostelma (1), Ischnostemma (1), Pseudibatia (2),
Steleostemma (1), Stigmatorrhynchus (1), Urostepha-
nus (1), Vailia (1)

GROUP C (9)

Tylophoreae-Ceropegiinae (9): Boucerosia (2), Caralluma
(3), Duvalia (1), Hoodia (6), Huernia (2), Huernio-
psis (2), Stapelia (12), Tavaresia (2), Trichocaul-
on (5).

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of caudicle to pollinia mostly subterminal or median;
P/C ratio usually less than 1.8; petal lobes not recurv-
ed.

GROUP C: Leafless cactus-like succulents; pollinia
reniform, large, horizontal with lateral inner tail; P/C
ratio often 1-2.4; petals stellate with short or indist-
inct lobes.

These are only the most conspicuous diagnostic featu-
res of groups A-C, and numerous other characters distin-
guishing between them could easily be extracted from the
data-matrix, although they are not of the same discrimi-
nating value as those mentioned above.

It is interesting to note that the present detailed

study has led to the subdivision of the Cynanchoideae in much the same way as achieved previously with a considerably smaller sample of plants (89 species from 33 genera) and characters by El-Gazzar, Hamza & Badawi (1974), who succeeded in recognizing the same 3 major groups A-C. This attests (though indirectly) to the taxonomic soundness of these groups: any groups based on 33 genera and can be easily expanded to accomodate 148 genera are of necessity taxonomically robust. Another useful aspect of groups A-C is that they provide a satisfactory pigeon holing system for 17 of the genera which have not hitherto been taxonomically catered for. Of these genera 5 are associated with members of group A, while the rest fall in group B.

It is clearly evident from Table 2 that Schumann's (1895) classification of the Cynanchoideae incorporates some homogeneous and some heterogeneous taxa. The former include the tribe Gonolobeae (in B), subtribe Tylophoreae Marsdeniinae (in B) and 2 of the 5 subtribes of the Asclepiadeae (Astephaninae in A and Oxypetalinae in B); all representatives of these taxa appear together in the same group although none of them emerged separately as a distinct assemblage. The heterogeneous taxa in Schumann's arrangement are the 4 subtribes Asclepiadeae Glossonematinae (with 7 genera in A and 6 in B), Asclepiadeae Asclepiadinae (with 19 genera in A and 11 in B), Asclepiadeae Cynanchinae (with 2 genera in A and 19 in B), and Tylophoreae Ceropegiinae (with 8 genera in B and 9 in C).

No attempt will be made here to formalize the present arrangement of genera since it is not based on the study of all known genera and species; clearly it would be futile to generalize the diagnoses given to groups A-C to cover genera on which they have not been based. However, we offer groups A-C as a reasonable taxonomic frame-work for this large subfamily of the Asclepiadaceae in the hope that future investigations might cover other genera not dealt with by us and further support our taxonomic ideas.

Acknowledgements

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